OVERWINTERING POTENTIAL IN CALIFORNIA OF TWO RUSSIAN WHEAT APHID PARASITOIDS (HYMENOPTERA: APHELINIDAE ET APHIDIIDAE) IMPORTED FROM CENTRAL ASIA

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Abstract.—*Aphelinus albipodus* Hayat and Fatima and *Diaeretiella rapae* (M'Intosh) (Hymenoptera: Aphelinidae and Aphidiidae) were imported to the USA for biological control of Russian wheat aphid (*Diuraphis noxia* Mordwilko) in 1992. Early laboratory studies identified potential limitations for their successful establishment in northern California where these parasitoids were extensively colonized and evaluated against Russian wheat aphid. Specifically, those studies showed that *A. albipodus* was particularly susceptible to moderately low temperatures (10° C). These results for *A. albipodus* were in contradiction with seasonal field temperatures prevalent in its collection site (Tahcheng, People's Republic of China) where field temperatures are below freezing for several months each year. This study sought to reconcile these apparently contradictory results. We examined whether short daylength-induced diapause, i.e. winter diapause, occurs in *A. albipodus* and *D. rapae,* and thus could be used as an overwintering strategy by these parasitoids. Under laboratory conditions, > ⅔ of *A. albipodus* individuals entered diapause when daylength was reduced from 14 h to 12 h. In contrast, diapause was not detected in *D. rapae* under the same conditions. However, we suggested that diapause may occur in *D. rapae* under shorter daylengths because (i) this parasitoid's development and survivorship are not affected by temperatures associated with 12 h daylengths at its collection site (Wuqia, PRC), and (ii) other studies have demonstrated diapause in this parasitoid at daylengths < 12 h. We discuss our results in light of *A. albipodus'* rapid establishment in northern California, and the use of our analytical procedure as a component of a process for screening natural enemies in importation biological control programs.

Key Words.—Insecta, *Aphelinus albipodus, Diaeretiella rapae,* diapause, biological control, *Diuraphis noxia,* establishment, importation.

Numerous biological control campaigns involving exotic natural enemies have been successful since the introduction of the vedalia beetle to California more than 100 years ago (DeBach & Rosen 1991; Greathead & Greathead 1992). Experience gained during that time and theoretical analyses have led to the identification of traits that presumably make natural enemies effective biological control agents (Huffaker et al. 1974, 1977; Beddington et al. 1978; Murdoch et al. 1985; Luck 1990; Murdoch & Briggs 1996). However, at this time it is uncertain whether these traits are useful or efficient for identifying the most promising natural enemies among a suite of available natural enemies (Luck 1990; González & Gilstrap 1992). In contrast, identifying natural enemies that offer promise for successful establishment in a new area seems a more tenable goal. Characterizing an exotic natural enemy's potential for establishment is important because lack of successful establishment precludes its eventual success in suppressing a pest population.

Climate (excessively cold, hot, or dry seasonal weather) is the single most

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frequently cited reason for natural enemy failure in biological control campaigns (Stiling 1993). Climate can early on limit a natural enemy's potential for success by impeding its permanent establishment following colonization. Close matching between the climates of collection and colonization areas of natural enemies used in classical biological control campaigns, i.e., *climate-matching,* is a long-standing conceptual "rule of thumb" for improving the chances of successful establishment of exotic natural enemies (Flanders 1940; Messenger 1959, 1971). It is unclear, however, how much emphasis is commonly placed on climate-matching in the planning phase of foreign exploration efforts. A comparatively information-intensive approach to climate-matching has been used successfully for forecasting range expansions of exotic pests (Messenger & Flitters 1954; Meats 1989; Hughes & Maywald 1990).

Shortly after the discovery of the Russian wheat aphid, *Diuraphis noxia* Mordwilko (Homoptera: Aphididae), in the USA in 1986, a biological control campaign involving several state, federal, and university agencies was organized against this pest. Numerous Russian wheat aphid natural enemies were imported to the USA as a result of this combined effort (Gilstrap et al. 1994). Based on information available from their collection areas, a limited suite of parasitoids was selected from among these natural enemies for evaluation in California (González et al., unpublished data). Among these parasitoids were *Aphelinus albipodus* Hayat and Fatima and *Diaeretiella rapae* (M'Intosh) (Hymenoptera: Aphelinidae and Aphidiidae, respectively). A series of studies identified potential limitations for successful establishment of these parasitoids in California (Bernal & González 1995, 1996, 1997; Bernal et al. 1997). In general, those studies suggested that *A. albipodus* was less tolerant of low temperatures than *D. rapae,* but the reverse was true at high temperatures. The implications of these results were that establishment in California of *A. albipodus* could be restricted by winter temperatures, but establishment of *D. rapae* could be restricted by summer temperatures. However, these results and their implications were in disagreement with available information concerning the climate of each of these parasitoid's collection areas (extremely cold and long winters, and moderate summers; see below). This was particularly true with regard to *A. albipodus'* susceptibility to low temperatures in the laboratory (Bernal & González 1996; Bernal et al. 1997), and its rapid establishment in northern California (González et al., unpublished data).

Based on these observations, we examined whether *A. albipodus* and *D. rapae* enter diapause in response to a short daylength, i.e., winter diapause. Entry into diapause under short daylength conditions would explain how these parasitoids survive the low temperatures prevalent during the late fall through early spring in their collection areas, and would influence their performance against Russian wheat aphid in California. Based on the results of this and previous studies we suggest that *A. albipodus* and *D. rapae* are able to survive the severe winters prevalent in their collection areas by entering a short daylength-induced diapause. In addition, we discuss how diapause and temperature-related developmental restrictions can affect the potential for successful establishment and the population dynamics of these parasitoids under California conditions.

Material and Methods

Parasitoid and Host Cultures.—*Aphelinus albipodus* and *D. rapae* were collected, respectively, near Tahcheng (46°42′ N, 83°00′ E, ca. 500 m elevation) and

Wuqia (Ulugqat) (39°05' N, 74°02' E, ca. 3000 m elevation), Peoples Republic of China, by D. González in 1992. The procedures for rearing Russian wheat aphid and both species of parasitoids were described earlier (Bernal & González 1993).

Experiments.—Two sets of trials were conducted for each of *A. albipodus* and *D. rapae*. The first set was designed to provide baseline information concerning emergence rates from mummies, and the maximum egg to adult developmental times in each of the parasitoids. The second set was designed to detect diapause if it occurred in either parasitoid species. The methodology for both sets of trials, and for both parasitoids, was similar, except that the daylength used in the second set of trials was shorter than in the first set of trials.

Previous studies showed that emergence rates from mummies at 21° C, 50–70% R. H., and 14 h daylengths were high (≥ 90%) in both *A. albipodus* and *D. rapae*. Thus, these environmental conditions (hereafter "non-diapause conditions") were used to obtain baseline information concerning emergence rates and developmental times in the first set of trials. Small pots of wheat, cv MIT, each covered with a small cage and containing ca. 40 Russian wheat aphids of instars III-adult (Bernal & González 1997) were exposed to 20 previously mated and fed, 1–2 day old female *A. albipodus* or *D. rapae*. The aphids were exposed to the female parasitoids for 24 h, after which the parasitoids were removed and the aphids were incubated under the non-diapause conditions described above. When aphid mummies formed, they were transferred each to a gelatin capsule (size #0) and further incubated under non-diapause conditions to allow emergence of adult parasitoids. The mummies were monitored daily for emergence of adult parasitoids, and the number of days from oviposition to emergence of individual adult parasitoids, the number of mummies formed, and the number of mummies yielding adult parasitoids from each pot were recorded. Fifteen pots with Russian wheat aphid were prepared for each of *A. albipodus* and *D. rapae*.

The second set of trials was similar to the first, except that the daylength was 12 h (hereafter "diapause conditions") rather than 14 h. In this case, 20 pots with Russian wheat aphid were used for *A. albipodus* and 15 pots for *D. rapae*. The results of the first set of trials showed that under non-diapause conditions, maximum egg to adult developmental times were 28 days in *A. albipodus* ($n = 344$), and 23 days in *D. rapae* ($n = 291$). Thus, for the second set of trials, mummies of each species not yielding adults within their corresponding maximum egg to adult times were tentatively considered to be in diapause. Emergence rates from mummies under diapause versus non-diapause conditions were compared via log-likelihood ratios for 2 × 2 contingency tables, with Yate's correction for continuity, for each of *A. albipodus* and *D. rapae* (Zar 1996).

Mummies under diapause conditions yielded fewer adult parasitoids than mummies under non-diapause conditions in *A. albipodus* but not in *D. rapae* (see *Results*). Whether the *A. albipodus* mummies that did not yield adult parasitoids under diapause conditions indeed contained diapausing individuals was determined via dissections. These mummies ($n = 242$) were divided into 2 groups of equal size at 28 days; one group was maintained under diapause conditions (i.e., 12 h daylength), the other was transferred to non-diapause conditions (i.e., 14 h daylength). Subsamples of mummies from each group were dissected at 48, 55, and 80 day from oviposition. Mummies containing live last instar parasitoid larvae

or pupae were considered to be in diapause. Both groups of mummies were further incubated if diapausing individuals were detected in the subsamples. The days to emergence, and the numbers of any parasitoids emerging from both groups of mummies were recorded.

Finally, the mean monthly temperatures and daylengths of each of the parasitoid's collection sites were compared versus a representative site from northern California, Tulelake (41°58' N, 121°28' W), where *A. albipodus* and *D. rapae* were colonized. Data for these comparisons were obtained from Walter & Lieth (1967), Pearce & Smith (1990), and Anonymous (1993).

RESULTS

The emergence rate of adult *A. albipodus* from mummies was significantly lower ($P \ll 0.001$) under the 12 h daylength relative to the 14 h daylength (Fig. 1). Less than ⅓ the proportion of *A. albipodus* adults emerging from mummies under the 14 h daylength emerged under the 12 h daylength. In contrast, emergence rates of *D. rapae* adults were similarly high and not significantly different ($P = 0.439$) under both daylengths (Fig. 1).

None of 121 mummies that were maintained at 12 h daylength for up to 84 days from the egg stage yielded *A. albipodus* adults. Dissection of these mummies revealed that they contained live last-instar larvae throughout this sampling period; 98% contained live last-instar larvae at 48 days from the egg stage ($n = 65$ mummies), 89% at 55 days ($n = 28$ mummies), and 93% at 80 days ($n = 28$ mummies). In contrast, ca. 12% of 121 mummies transferred from 12 h daylength to 14 h daylength at 28 days from the egg stage yielded *A. albipodus* adults within 47–75 days.

Dissection of five of the mummies transferred to 14 h daylength at each of 48, 55, and 80 days from the egg stage indicated that the remaining mummies contained living last-instar larvae (15/15 total mummies dissected contained live last-instar larvae). Although additional adult emergence from the mummies transferred to 14 h daylength was plausible given the prevalence of live last instar larvae inside these mummies after 80 days, these were accidentally destroyed at 84 days when a mechanical failure caused a sudden increase in the ambient temperature to >40° C for ca. 20 h.

DISCUSSION

Our results showed that *A. albipodus* entered diapause when it developed under a 12 h daylength. The incidence of diapause in *A. albipodus* at this daylength, discounting for mummy stage mortality evident under the 14 h daylength (ca. 8%), was ca. 68%, and it occurred in the last larval instar. In addition, our results showed that diapause could be broken in some *A. albipodus* individuals by exposing diapausing mummies to a 14 h daylength. In contrast to *A. albipodus, D. rapae* did not enter diapause when it developed under a 12 h daylength.

Our findings concerning *A. albipodus* were not unexpected, whereas those concerning *D. rapae* were initially puzzling given the climatic conditions prevalent in their areas of origin (Fig. 2). Mean monthly temperatures at Tahcheng, *A. albipodus*' collection site, vary from −16° C in January to 22° C in July, and daylengths vary from 8.5 h in December to 15.9 h in June. Temperature conditions in Wuqia, *D. rapae*'s collection site, are less extreme than in Tahcheng, ranging
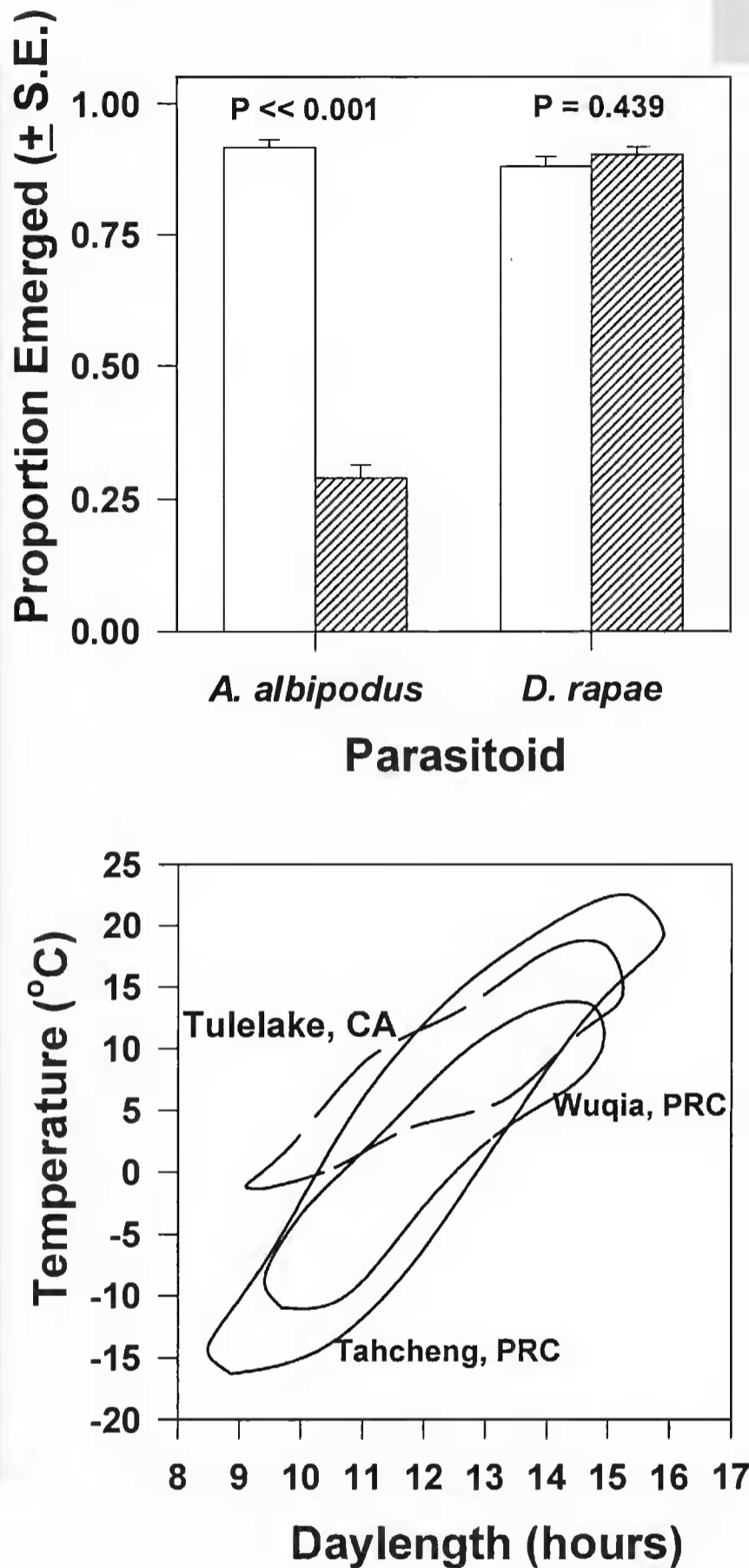
Figure 1.   Emergence rates of *Aphelinus albipodus* and *Diaeretiella rapae* under two daylengths (21° C, 50–70% R.H.); hollow columns = 14 h daylength, stippled columns = 12 h daylength. Numbers above column pairs indicate significance of difference in emergence rates between 14 h and 12 h daylengths: *A. albipodus*, G = 306.470, 1 df, n = 685; *D. rapae*, G = 0.666, 1 df, n = 719.

Figure 2.   Daylength (on the 15th of each month) and mean monthly temperature variation in: Tahcheng, People's Republic of China, *Aphelinus albipodus*' collection site; Wuqia, PRC, *Diaeretiella rapae*'s collection site, and; Tulelake, California, a representative northern California colonization site for *A. albipodus* and *D. rapae*.

from $-11°$ C in January to $13.5°$ C in July, while daylengths are similar, 9.4 h in December to 14.9 h in June. Despite differences in temperature, winter conditions in both Tahcheng and Wuqia would require a mechanism by which *A. albipodus* and *D. rapae* could survive during 5 months of subfreezing mean monthly temperatures.

Diapause provides a mechanism for winter survival in *A. albipodus*. Mean monthly temperatures and average daylengths in Tahcheng closely match temperature- and daylength-related developmental restrictions in *A. albipodus* that are evident from this and other studies (Bernal & González 1996; Bernal et al. 1997). Those studies showed that *A. albipodus:* (i) enters diapause at 12 h daylengths, and; (ii) cannot develop to adulthood if temperatures are $10°$ C or below. *Aphelinus albipodus* mortality at $10°$ C is $>80\%$ during egg to mummy development, and adults do not emerge from mummies that develop at this temperature (Bernal & González 1996; Bernal et al. 1997). Mean temperatures in Tahcheng decrease to $10°$ C and below in the fall, and are associated with 12 h and shorter daylengths. Mean temperatures then increase to $10°$ C and above in the spring and are associated with 14 h and longer daylengths. Thus, *A. albipodus* may avoid fatally low temperatures by entering diapause when daylengths decrease to 12 h in the fall, then resuming development when daylengths increase to 14 h in the spring.

In contrast to *A. albipodus,* diapause was not detected in *D. rapae* at 12 h daylength. Based on our results, however, we cannot discount the possibility of diapause in this parasitoid. *Diaeretiella rapae* populations in the Netherlands enter diapause during the winter (Hafez 1961). Moreover, diapause in these *D. rapae* populations peaks in late October (Hafez 1961) when daylengths are between 10.7 and 8.8 h. Thus, diapause may be induced at daylengths shorter than 12 h in the Wuqia *D. rapae* population. Average daylengths in Wuqia decrease to 12 h in the early fall and are associated with mean temperatures of ca. $7°$ C. Later in the fall, mean temperatures decrease to subfreezing levels, but daylengths by then decrease to 10.5 h and shorter. Previous studies show that developmental mortality in *D. rapae* is low at $10°$ C, and that its lower developmental threshold is in the range $2.5-3.9°$ C (Bernal & González 1995, 1997). Thus, diapause at 12 h daylength in the Wuqia *D. rapae* population may not be necessary given the associated mean field temperatures (ca. $7°$ C) in the area. Hence, based on the results of previous studies (Hafez 1961; Bernal & González 1995, 1997) and on the lengthy and severe winters prevalent in Wuqia, a likely scenario is that diapause in *D. rapae* is induced by daylengths shorter than 12 h, which are associated with near- or sub-freezing temperatures.

Our results concerning *A. albipodus* are consistent with previous reports of diapause in closely related *Aphelinus* spp. Yu (1992) found that $>50\%$ and $>95\%$ of *A.* nr. *varipes* (= *A. varipes,* see Bernal et al. 1997; J. B. Woolley, personal communication) collected in southern Alberta (Canada) entered diapause when they developed under 14 h and 12 h daylengths, respectively. The corresponding rates for *A. varipes* collected in Kazakhstan (= *A. albipodus,* see Bernal et al. 1997; J. B. Woolley, personnel communication) were 0% and $>90\%$. Diapause was induced by short daylengths both in Yu's and this study. Short daylengths in these cases are associated with low winter temperatures that may be particularly detrimental to *Aphelinus* species. Developmental thresholds and high mortality at temperatures between 5 and $10°$ C are common in *Aphelinus* spp. (e.g., Force &

Messenger 1964; Walker et al. 1988; Trimble et al. 1990; Asante & Danthanarayan 1992; Lajeunesse & Johnson 1992; Yu 1992; Bernal & González 1993, 1996; Bernal et al. 1997; Lee & Elliot 1998a, b). Thus, *Aphelinus* spp. appear to be highly susceptible to low temperatures and to employ diapause as an overwintering strategy (Trimble et al. 1990; Yu 1992; this study).

Both *A. albipodus* and *D. rapae* were imported to California for release against Russian wheat aphid (González et al., unpublished data). Both were extensively released in northern California and *A. albipodus* rapidly became established. It is unclear at present whether *D. rapae* became established because this species already occurred in the area. In either case, it is evident that the climate in northern California is milder during the winter relative to the collection areas of both parasitoids, and daylength variation during the year is similar between these areas, or less in the case of *D. rapae* (Fig. 2). Thus, although diapause may be induced by short winter daylengths in northern California, it may not be required for winter survival of *A. albipodus* and *D. rapae*. Summer, rather than winter, temperatures may represent an obstacle for establishment of *D. rapae,* in particular, in northern California. Earlier studies showed that *D. rapae* is more susceptible to high temperatures than *A. albipodus* (Bernal & González 1995, 1996). This is suggested also by the seasonal variation in mean temperatures in each of these parasitoid's collection sites. Thus, winter diapause and summer survival are two important factors that may affect the population dynamics of *A. albipodus* and *D. rapae* and their impact on Russian wheat aphid populations in California. Moreover, the timing of emergence of diapausing parasitoids in the spring will likely influence their impact on Russian wheat aphid populations. Previously it was suggested that in annual agroecosystems, early-appearing natural enemies are likely to have a greater impact on pest populations than those emerging later in the season (Bernal & González 1993; Gilstrap 1997). Our results, and previous studies (Bernal & González 1995, 1996), suggest that *A. albipodus* is likely to emerge later in the season than *D. rapae.*

Differences in climate between collection and colonization areas of exotic natural areas are reported to contribute substantially to reducing the success rate of classical biological control (Stiling 1993). Specifically, they hamper biological control efforts early on in their development by precluding the successful establishment of exotic natural enemies. A practice that could contribute substantially to reducing the number of biological control efforts that fail during the colonization phase is to emphasize closer climate-matching during the planning phase of foreign exploration efforts. An approach similar to that taken to forecast potential range expansions of pest species (Meats 1989; Hughes & Maywald 1990) would be desirable, but may seldom be possible with exotic natural enemies. Unlike pest species, usually little or no information is available concerning an exotic natural enemy's response to temperature and other biological parameters necessary for such an approach. Many times exotic natural enemies are undescribed species and biological information can only be inferred from related species; other times, the available information is limited to a taxonomic description. In both cases, pertinent biological information becomes available only after a series of studies are conducted. We believe that the analyses presented here, including the results from previous studies (Bernal & González 1995, 1996, 1997; Bernal et al. 1997), provide an initial model for assessing the potential for suc-

cessful establishment of exotic natural enemies early in the development of a biological control campaign, and a means for improving the success rate of classical biological control. Ultimately, the success of a classical biological control campaign is contingent upon the successful establishment of exotic natural enemies.

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